

Arizona collections by C. Leathers (personal communication to H. D. Thiers), is of interest since Singer (1948; 1962), Smith (1949), and Smith (1954) all reported their absence. Preliminary anatomical examination of collections from other parts of the United States (Sundberg and H. D. Thiers, in preparation) has verified the presence of clamp connections in this species. This evidence indicates that they were probably overlooked by previous workers and their absence cannot be used, as had been by Singer (1948; 1962), in support of the generic segregation of *Chlorophyllum* from closely allied species of *Lepiota* sensu lato.

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Note added in proof. Recently clamp connections were reported in *C. molybdites* from Tennessee and Israel (Heinemann, P. Bull. Jard. Bot. Etat 38:195–206. 1968) and from Africa and South America (Singer, R. Beih. Nova Hedwigia 29:1–405. 1969).

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POLYPHYLETIC ORIGIN OF TETRAPLOID POPULATIONS OF *GUTIERREZIA SAROTHRÆ* (COMPOSITÆ)

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The widespread western North American species *Gutierrezia sarothrae* (Compositae—Astereae) possesses two chromosomal races: a diploid ($n = 4$) race that is the most common, and a less common tetraploid ($n = 8$) race, that comprises approximately 20% of populations. Both races are morphologically very similar. Although the polyploids tend to have statistically slightly larger pollen and stomata, there is no single character by which the two races can be separated (Solbrig, 1964). This is due to a great deal of variability in both the diploid and tetraploid forms. Neither can the two races be separated on the basis of geographical distribution since the tetraploid populations occur interspersed throughout the distribution of the species.

In a previous paper (Solbrig, 1964) I suggested that polyploids may have arisen from diploids more than once. This would tend to explain their morphological diversity and geographical distribution. The major reason for making this suggestion, was that at any one locality where polyploids occurred, they tend to show the expected "gigas" characters in relation to the diploids of that area. However, the diploid populations of another region are not necessarily smaller. In the present paper further evidence in favor of the hypothesis of a polyphyletic origin of the polyploid populations is presented as a result of a numerical analysis of relationships among the populations.

MATERIALS AND METHODS

The data collected in previous studies (Solbrig, 1960; 1964; 1965) were utilized in the present analysis. The OTU is the breeding population. The characters used are the mean value obtained after measuring 13 characters in 50 individual plants chosen at random in a population. For this study data from 15 diploid ($n = 4$), 5 tetraploid ($n = 8$) and 14 populations of unknown chromosome number of *G. sarothrae*, as well as 3 tetraploid ($n = 8$), 1 hexaploid ($n = 12$) and 1 of unknown chromosome number of *G. bracteata*; 1 diploid ($n = 4$) population of *G. serotina* and 1 hexaploid ($n = 12$) population of *G. serotina* and 1 hexaploid ($n = 12$) population of *G. californica*; and 2 tetraploid populations of *G. microphala*, were utilized (table 1). The data were processed on an IBM 7090 Computer at the University of Michigan Computing Center.

Two numerical analyses were used. One, the Prim Network (Prim, 1957), is essentially a coefficient of similarity in a multidimensional space that produces a linear clustering of OTU's. The second is a program that produces a phylogenetic tree following the principle of parsimony, where species are derived from a given ancestor along the most parsimonious paths (Kluge and Farris, 1969; Wagner, 1961).

RESULTS

Figure 1 depicts graphically the Prim Network that was obtained. It can be seen that the variability of the species follows three major lines. First, a line that is characterized by a tendency towards smaller heads with a reduced number of florets per head and that culminates in populations of *G. microcephala* that have only 1 ligulate and 1 tubular florets. Of the 16 populations in this line, 6 are diploid, 3 are tetraploid (including both populations of *G. microcephala*) and seven are of unknown chromosome number. Ten of the populations come from the southeast area of the distribution of these species, that is, the area comprised by Colorado, New Mexico, Oklahoma and Texas. The other six populations come from Utah, Wyoming, Kansas and South Dakota.

The second direction exhibited by the pattern of variation is toward an increase in head size with accompanying increase in the number of florets. Only three populations of *G. sarothrae* are involved, together

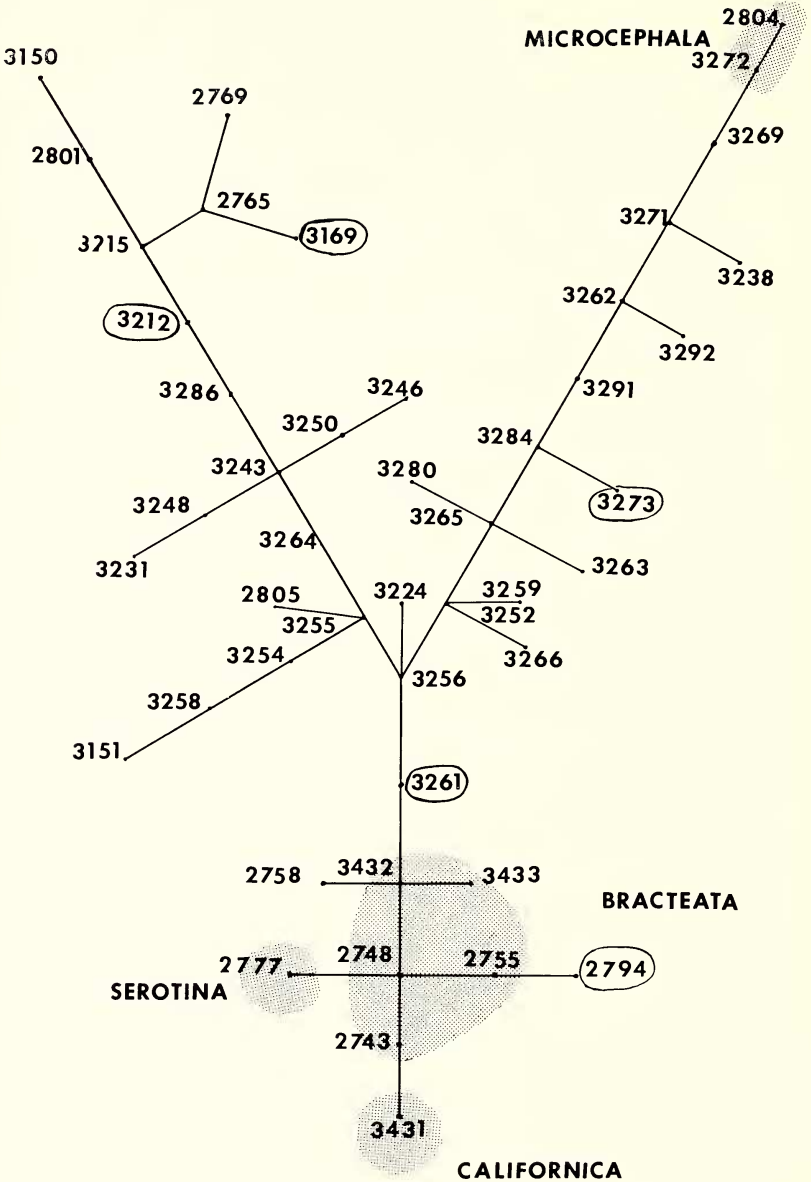


FIG. 1. Prim network of the populations studied. The lines separating any two populations represent the phenetic distances. The angles are arbitrary, and distances between populations other than along the drawn lines non-significant. All populations that are not shaded are *Gutierrezia sarothrae*, those encircled in a balloon are tetraploid with $n = 8$; all other *G. sarothrae* are either diploids or of unknown chromosome number (see table 1).

TABLE 1. LOCALITIES SAMPLED FOR THIS STUDY AND CHROMOSOME NUMBERS. Collection numbers are those of the author and specimens are in the Gray Herbarium.

Gutierrezia bracteata. California: Cache Creek, 3432; Arroyo del Puerto, 3433, n = 8; Arroyo del Puerto, 2743, n = 8; Pond Ranch, 2748; Temblor Range, 2755.

Gutierrezia californica. California: Point Bonita, 3431, n = 12.

Gutierrezia microcephala. Arizona: Hyde Park, 2804; New Mexico: White City, 3272.

Gutierrezia sarothrae. Arizona: Payson, 2794, n = 8; Ash Fork, 2801, n = 4; Hyde Park, 2805, n = 4. California: near Temecula, 2768, n = 4; near Chula Vista; 2776, n = 4; near Rancho Santa Fe, 2769, n = 4. Colorado: Colorado National Monument, 3261, n = 8; Colorado National Monument, 3262, n = 4; near Salida, 3263; near Fountain, 3264; near Trinidad, 3265. Idaho: near Dubois, 3254, n = 4; near Pocatello, 3255. Kansas: near Medicine Lodge, 3292, n = 4. Montana: Glendive, 3248; Sanders, 3250, n = 4. Nebraska: Roscoe, 3224, n = 4; near Chadron, 3231. New Mexico: near jct. highways 285 and 286, 3169, n = 8; near Glenwood, 3215; near Las Vegas, 3266; near Roswell, 3269, n = 4. North Dakota: Dickinson, 3243; Little Missouri R. and highway 85, 3246. Oklahoma: near Bouse Jct., 3291. South Dakota: near Rapid City, 3238. Texas: near Van Horn, 3212, n = 8; near White City, 3271, n = 4; near Van Horn, 3273, n = 8; near Alpine, 3280, n = 4; near San Angelo, 3284; near Abilene State Park, 3286, n = 4. Utah: near Boulder, 3150, n = 4; near jct. highways 24 and 6, 3151, n = 4; near Ogden, 3256; near Vernal, 3258, n = 4; near Talmadge, 3259.

Gutierrezia serotina. Arizona: Tucson, 2777, n = 4.

with all the populations of *G. bracteata*, *G. californica* and *G. serotina* that were analyzed. Two of the three populations of *G. sarothrae* that exhibit this pattern of variation are tetraploid; in addition all populations of *G. bracteata* and *G. californica* are either tetraploid or hexaploid, so that of 10 populations involved, 2 are hexaploid, 5 are tetraploid, 2 are diploid and one is of unknown chromosome number. All but one of the populations grow in either Arizona or California. The exception is population 3261, a tetraploid *G. sarothrae* from Grand Junction, Colorado.

The remaining 21 populations, all of them *G. sarothrae*, comprise what may be called "typical" *sarothrae*. Geographically they come from throughout the range of the species, including California and Texas. Chromosomally 8 populations are diploid, 2 tetraploid and eleven are of unknown ploidy level.

Figure 2 depicts the phylogeny produced by the Farris program. For purposes of this analysis, population 3256 of *G. sarothrae* which exhibits characters at the center of the species variability in the Prim Network was chosen arbitrarily as exhibiting the most primitive characters. Runs were made using other populations as primitive. This produced different shaped trees, but no variation in the basic relations of the populations to each other. According to the phylogenetic tree produced by this program, there are three evolutionary tendencies within *G. sarothrae* that follow roughly the lines of variation uncovered by the PRIM diagram: one is a tendency towards smaller heads with fewer flowers that culminates in *G. microcephala*; the other is a tendency towards larger heads that culminates in *G. bracteata* and *G. californica*, and the third is also

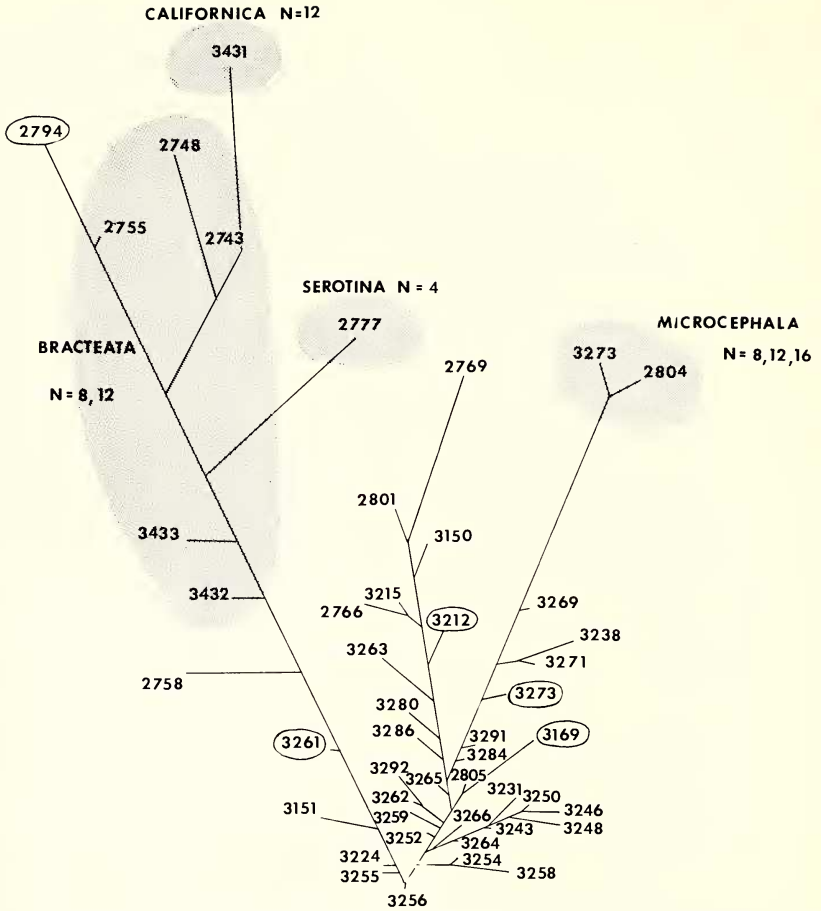


FIG. 2. Hypothetical phylogeny following the most parsimonious lines drawn by a computer following a program devised by J. A. Farris (Kluge, 1969). Non-shaded populations are *G. sarothrae*; those included in a balloon are tetraploids with $n = 8$; all other *G. sarothrae* are either diploid or of unknown chromosome number (see table 1).

a tendency towards larger plants with larger heads not connected to the previous one. *Gutierrezia californica* appears to be the most modified of the species analyzed; the line that culminates in *G. microcephala* follows. These numerical indices tend to confirm the taxonomic treatment with one exception: population 2794 from Arizona appears to be related both in its pattern of variation and in its hypothetical phylogenetic history to *G. bracteata*, and probably should be classified as such. Blake in the Flora of Arizona (Kearney and Peebles, 1942) classified the large headed Arizona populations as *G. californica* (= *G. bracteata*). This would extend the range of this species, previously considered by me (Solbrig,

1965) as restricted to California and Baja California. Of greater interest for our present discussion, is that polyploid populations are found in all three of the phylogenetic lines.

DISCUSSION

The present numerical analysis tends to confirm the hypothesis that tetraploid populations of *G. sarothrae* have arisen and become established in more than one instance. This would explain the geographical dispersion of the tetraploids, and also the fact that they cannot be separated as a group from diploids also taken as a whole. However, when tetraploid populations are compared to the diploid populations to which they are most closely related within each of the three major lines of variability, they show the expected "gigas" characteristics (fig. 1). This analysis permits us to obtain a reasonable idea of the evolutionary patterns within a species. From the "typical" or "modal" population it appears that a line with larger heads and more flowers developed in the southwest United States that eventually lead to the formation of three species: *G. serotina*, *G. bracteata* and *G. californica*. On the other hand, in the southeast part of the range, forms with narrower heads and fewer flowers were selected that lead to the formation of *G. microcephala*, a species that eventually became widespread over all of southern United States and northern Mexico. It is impossible to affirm that polyploidy provided the isolating barrier in these instances and aided the selective trends, but it appears to be a plausible hypothesis.

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